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Annual Phytoplankton Metabolism in Narragansett Bay Calculated from Survey Field Measurements and Microcosm Observations

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ABSTRACT: Field surveys of phytoplankton metabolism, based on oxygen changes, were made in Narragansett Bay from 1971–73. Annual daytime net production varied from 218 g C per m^2 per yr in the East Passage to 429 g C per m^2 per yr in the Providence River. The area based average for the bay was 269 g C per m^2 per yr. The area based average night respiration was 159 g C per m^2 per yr resulting in an annual net carbon available for export or to the benthos of 110 g C per m^2 per yr. A set of microcosms, operated so as to simulate the Bay, had an annual net production of 276 g C per m^2 per yr and a night respiration of 163 g C per m^2 per yr resulting in an annual net carbon available for export or to the benthos of 113 g C per m^2 per yr.

Introduction

Despite long and intensive study of the ecology of Narragansett Bay, Rhode Island, measurements of *in situ* annual metabolism of the bay as a whole have not been reported. After the long history of primary productivity estimates, one might expect that this measurement is a simple textbook exercise, but these estimates are still difficult. In the oxygen light and dark bottle technique, net production includes the respiratory losses due to phytoplankton but, depending on the study, it must also include respiratory losses of some sizes of pelagic heterotrophic organisms. The term "apparent production" in total system measurements includes, in addition to pelagic heterotrophic respiration, the respiration of the benthic community during the day. The use of the carbon-14 technique leads to new difficulties: when corrected for dark bottle uptake it measures the uptake of carbon during photosynthesis by phytoplankton, but it is not quite equivalent to the net production measured by the oxygen technique, and the daytime carbon uptake pattern is different from the oxygen release pattern (Harris 1978). Other difficulties include variations due to different periods of incubation, and the question of *in situ* incubations versus incubations in a light gradient box, and more. We have struggled with some of these problems but it is not our purpose here to review the problems of primary productivity measurements; suffice it to say that after more than three quarters of a century we are able to relate primary productivity to fish production with only rough accuracy.

In the bay, a strong eutrophication gradient exists between the nutrient laden Providence River and the relatively oligotrophic Rhode Island Sound (Kremer and Nixon 1978). It was expected that there should be a corresponding productivity gradient. The greater depth of the East Passage (15 m) compared to the West Passage (7 m) may also result in a different productivities. A bay-wide estimate which takes into consideration the different productivities of different areas should be more accurate than past estimates.

In this study the net primary production (including the negative contribution by heterotrophic pelagic respiration) of Narragan-

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sett Bay was surveyed using the oxygen light-and-dark bottle technique. These survey estimations were compared to measurements made in the microcosms at the Marine Ecosystems Research Laboratory (MERL), University of Rhode Island. The microcosms are 5 m deep and contain 13 m^3 of water, and have been scaled so as to be surrogates of Narragansett Bay to the extent that is at present feasible (Pilson et al. 1979; Pilson et al. 1980; Nixon et al. 1980). In part this comparison should reveal how well they have been scaled.

Methods

Survey

Approximately monthly during the summer and less frequently in other seasons, surveys of *in situ* primary production were made at 12 stations in Narragansett Bay from 1971 to 1973 (Fig. 1). During 1971 oxygen light and dark bottles (300 ml) were incubated in duplicate 1 m beneath the surface and 1 m off the bottom. Water for the incubations was collected from the respective depths. Incubations were from 3 to 5 hours during midday. During the next two years the incubations were made only 1 m beneath the surface. All bottles were pickled immediately and titrated for oxygen concentration (Strickland and Parsons 1968) within 24 hours of the incubations, resulting in metabolism values in g 0_2 per m^3 per hr. Error of the titration was ± 0.03 g per m^3.

During 1972 and 1973, 27 vertical profiles of production over the water column were obtained to develop a relationship for converting survey values to water column values. Fourteen of these profiles were made in 4.5 m water off the Graduate School of Oceanography (GSO) dock; the rest were made at random locations around Narragansett Bay (Fig. 1). Duplicate light bottles were positioned at 0.05 m, 0.25 m, 0.50 m, and every 0.50 m thereafter; two dark bottles were incubated at the bottom and at 0.05 m. All water for these incubations was collected at the surface. In a stratified water column the surface phytoplankton assemblage may be different in light adaptation, density, and speciation from the assemblage at depth. However, most of the bay is not strongly stratified (Hess and White 1974).

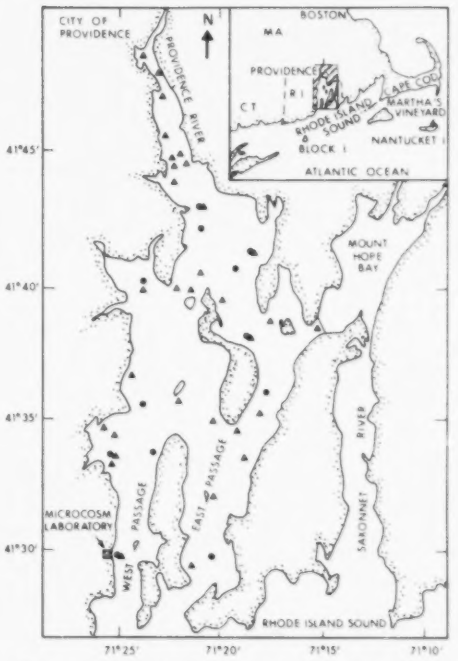

Fig. 1. Oxygen incubation stations in Narragansett Bay 1971–73, ● sampling stations for profiles. ▲ regular sampling stations for 1 m incubations. △ occasional sampling stations for 1 m incubations.

Further there is no evidence for consistent differences between the concentrations of phytoplankton or nutrients in surface and bottom water (see Figs. 4 and 5 in Kremer and Nixon 1978). Incubations were from 3 to 5 hours long during midday. Depth-integrated production was obtained by plotting the data by depth and measuring the area under the resulting graph. On the average these profiles indicated that net production over the water column (per m^2) was 3.41 ± 1.26 times the net production (per m^3) at 1 m (Table 1). This factor increases with depth of the euphotic zone which varies between 2 and 8 m; for example, at the one station at 20 m depth it was 4.77. The depth of the 1% light level in the bay usually occurs between 4 and 5 m.

Microcosm Total System Metabolism

Oxygen concentration was measured early in the morning and late in the afternoon to calculate diel apparent production and

TABLE 1. Summary of bay survey conversion factors.

A.	Net Production over the water column (g $O_2/m^2/hr$) = 3.41 × g $O_2/m^2/hr$ at 1 m) (n = 27, s/x = 37%, Z from 4.5 to 20 m)
B.	Daily Net Production over the water column g $O_2/m^2/day$ = net production from 1000 to 1400/0.57 hr, n = 22
C.	Night Respiration Annual bay day time production ÷ 1.69 = annual bay night respiration (MERL microcosms 5 and 7, August 1978 to August 1979, had an annual water column ratio P_{day}/R_{night} = 1.69)
D.	Oxygen to Carbon Carbon = (12/32 ÷ 1.21) × Oxygen = 0.31 × Oxygen (using photosynthetic quotient (P.Q.) of 1.21)

night respiration (Odum and Hoskin 1958). Two tanks were measured once a week from August 1978 to August 1979. All nine tanks were measured from November 1978 to August 1979. Duplicate water samples were taken from each tank during tank mixing. Samples were titrated by the Winkler titration within 24 hours. Oxygen diffusion measurements were made (Nixon et al. 1980) and these diffusion corrections were made to all total system measurements. Production and respiration values were graphed from August 1978 to August 1979 and integrated.

Metabolism Partition in the Microcosms

Total system, phytoplankton, and benthic metabolism were measured nearly concurrently in two microcosm tanks in June, July, August and October 1978. Total system metabolism and plankton metabolism were measured by the diel curve method (as above with more frequent samples) and by hanging light bottles (60 ml) at various depths in the tanks. Dark bottles were hung only at the surface. These bottles were changed every 4 hours over the 24 hour periods. Before sampling the microcosms, the mixers were turned on for 10 minutes to mix the water column to homogeneity (Nixon et al. 1980). Oxygen samples were titrated within 24 hours. Benthic respiration was measured *in situ* in the microcosms during the same months. A circular plexiglass chamber (1.76 m in diameter and 12 cm high) was designed to fit over the entire sediment surface in the microcosms. Incubations for measurement of respiration were 2 to 4 hours long. Initial and final samples were siphoned through a sampling hose. Three control bottles were incubated at the same depth and the data used to correct for pelagic respiration. After incubation, PVC rods were dropped from the surface of the chamber to the surface of the sediment to obtain a measure of water volume enclosed by the chamber. A stirring bar within the chamber was gently turned by hand prior to sampling the enclosed water column. The analytical precision of the oxygen measurements and the resulting effect on oxygen fluxes for a 3 hour incubation were: O_2 ± 0.03 g per m^3 or ± 1.7 mg per m^2 per hr.

Factors for Correcting Bay Survey

Factors for converting 3- to 5-hour bay incubation values to estimates of daily production and night respiration were derived from microcosm studies in the MERL tanks. Production estimations in the tanks were made for the light period of the day and comparisons of the amount of midday production to total daily production were made. In these incubations, 57% ± 13% of the daily net phytoplankton production occurred from 1000 to 1400 hr (Table 1). In a year-round salt marsh embayment study this value was 58% ± 14%, n = 15 (Nixon and Oviatt 1973). Both of these values fall within Vollenweider's (1965) range of 55–60%.

Thus factors converting the values of production derived from 4 hr incubations in bottles at a depth of 1 m during the bay survey to estimates for the whole water column and over the daily period were obtained

(Table 1). These factors were applied to some 24 average values of daytime production from incubations in the West Passage, the East Passage, and the Providence River during 1971 to 1973. Each average value was derived from 3 to 5 individual incubations. The estimates of daily rates were plotted over the annual cycle and the areas under the resulting curves integrated. The spring bloom occurred during different periods in the two years. When there were enough points to calculate two different values, the two yearly values were averaged.

Respiration estimations have presented a greater difficulty. Many of the respiration values from the bay survey were low and within the titration error and, therefore, these values were not used. Instead the MERL water column ratio of daytime production to nighttime respiration for the year have been applied to the annual bay survey production values (Table 1). (The derivation of this ratio is fully explained in the results section under microcosms.) In doing this we have had to assume that the respiration occurring on a 5 m MERL water column was equivalent to the 10 m bay water column. During the 1971–72 bay survey respiration was measured at the surface and bottom 46 times. However, in only 8 of these measurements were the rates sufficiently high (>0.04 mg O_2 per l per hr) to be reliable. In these 8 measurements in a mean depth of 6 m the average respiration of the bottom was 69% ± 27% of that of the surface, providing some evidence that the respiration decreased at depth in the bay water column. This pattern would probably have to be the case for the microcosms and the bay to be equivalent. Both water column and 24 hour patterns of plankton respiration are poorly understood (Sournia 1974).

Oxygen to Carbon Conversion

The conversion of oxygen to carbon was made by choosing a photosynthetic quotient (P.Q.) of 1.21. This value for the P.Q. was at the midpoint of the range of 1.1 to 1.3 in Ryther (1965) as quoted in Parsons, et al. (1977). From the relationship O_2 production (12/32)(1/P.Q.) = Carbon production, we calculate the ratio of carbon production to oxygen production as 0.31 (Table 1).

TABLE 2. Mean phytoplankton daytime net production in Narragansett Bay. Each value is the mean from 3–5 stations incubated at 1 m in the region on the specified day. Calculation procedures are described in text and Table 1.

Date	West Passage Net Production g O_2/m²/day	East Passage Net Production g O_2/m²/day	Providence River Net Production g O_2/m²/day
6/15/71	1.78	—	—
6/29/71	4.36	3.08	—
7/7/71	3.36	4.22	1.33
7/28/71	4.70	2.08	11.6
8/5/71	4.84	5.12	—
8/17/71	5.69	4.66	—
8/25/71	—	—	17.8
9/8/71	4.27	—	8.24
10/20/71	2.15	3.46	0.00
1/27/72	1.54	3.79	2.34
3/9/72	3.69	3.40	2.67
4/19/72	1.48	1.78	1.33
5/26/72	2.85	2.73	1.29
5/31/72	5.26	—	—
7/5/72	6.36	3.39	4.78
10/5/72	7.04	4.58	1.23
11/15/72	0.24	0.12	0.05
12/14/72	0.35	0.47	0.00
1/10/73	0.23	0.07	0.08
2/13/73	0.82	0.18	0.10
3/8/73	2.98	5.14	2.40
3/13/73	2.90	0.96	—
4/19/73	8.20	—	5.03
6/13/73	1.33	1.71	5.73
Mean coefficient of variation	81%	75%	104%

Results

Bay Metabolism

Means for net production for each date are presented in Table 2. Generally from 2 to 6 g O_2 per m² per day were produced during the summer in the West and East Passages. Occasionally much higher values were obtained in the eutrophic Providence River. Production during the winter was generally less than 1 g O_2 per m² per day except during periods of the spring bloom, which occur before there has been significant warming. With the titration error production has an associated error of ±0.18 g O_2 per m² per day. Some of the winter values are below these limits of detection.

The best data set for illustrating short term variation, seasonal variation, and to some extent, annual variation at one station was obtained off the dock at GSO (Fig. 2). Net production values included data from

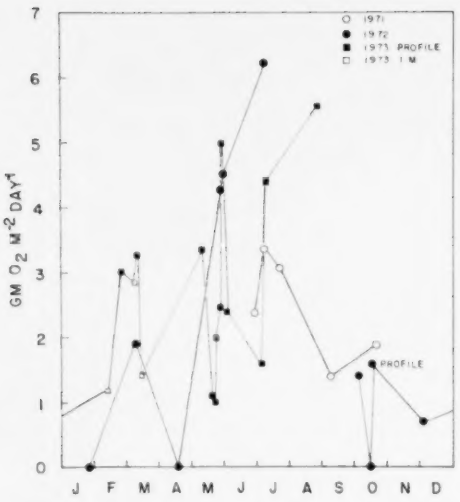

Fig. 2. Daily net production at the dock at the Graduate School of Oceanography over the annual cycle. Open circles indicate 1971 survey at 1 m; closed circle indicates 1972 survey at 1 m but there was one profile as indicated; closed box indicates 1973 profile measurements and open box indicates 1973 survey at 1 m.

14 profiles as well as 17 1 m incubations. Rapid changes in metabolism were observed during close interval sampling in May. Most of the data presented in Table 2 came from sampling carried out at biweekly to monthly intervals. This sampling scheme undoubtedly missed a lot of the fine structure associated with phytoplankton blooms. Production values were highest during the summer and lowest during the fall and winter, but rose during the period of the winter-spring bloom. The timing and period of the winter-spring bloom and the presence or absence of a fall bloom contribute to year-to-year variability. Variability due to patchiness must also be a factor contributing to high coefficients of variation (Table 2). Concurrent sampling over large areas such as the several parts of the bay would tend to average out such variability. Values in Table 2 were used to estimate integrated annual values.

Estimated daytime net production in Narragansett Bay during 1971–73 was 868 g O_2 per m^2 per year or 269 g C per m^2 per year (Table 3). At two locations there were sufficient data to calculate two annual values. The one-year values departed from the two-year means by $\pm 13\%$ at the GSO dock and $\pm 16\%$ for the Providence River. The estimated whole bay night respiration was 159 g C per m^2 per year, based on the microcosm P/R of 1.69 (Table 1). Along the eutrophication gradient from the Providence River to the mouth of the bay, highest values of metabolism occurred in the Providence River and the average West Passage value was higher than the value from the GSO dock in the lower West Passage. Nutrient concentrations were generally lower in the East Passage than in the West Passage due in part to a deeper water column in the East Passage and greater exchange with the relatively oligotrophic Rhode Island Sound (Kremer and Nixon 1978). Correspondingly, metabolism values were lower in the East Passage than in the West Passage.

Microcosm Comparison

In two tanks total system metabolism was measured from August 1978 to August 1979. Since November 1978 it has been routinely

TABLE 3. Yearly integrated metabolism for Narragansett Bay 1971–73 and net carbon available for export and to the benthos.

	Production ± (Range) g $O_2/m^2/yr$	Production g $C/m^2/yr$[a]	Night Respiration g $C/m^2/yr$	Net Carbon g $C/m^2/yr$
West Passage (n = 80)	893	277	164	113
Dock, GSO (n = 31)	714 (618–810)	221	132	89
East Passage (n = 64)	703	218	129	89
Providence River (n = 79)	1,385 (1,169–1,601)	429	254	175
Area based average	868	269	159	110

[a] See Table 1 for method of conversion.

TABLE 4. Integrated total system metabolism in two micrososms (August 1978 to August 1979) and that metabolism corrected for sediment respiration to be comparable to bay measurements.

	Microcosm Metabolism g $O_2/m^2/yr$ $\bar{x}$ (Range)	Microcosm Metabolism Plus Sediment Respiration[a]	
		g $O_2/m^2/yr$	g $C/m^2/yr$[b]
Apparent Production	631 (621–641)	890	276
Night Respiration	462 (453–471)	525	163
P_{day}/R_{night}		1.69	
Carbon available to benthos (P-R)			113

[a] See text for explanation.
[b] See Table 1 for method of conversion.

measured in 9 tanks, but tanks were drained, cleaned, and filled with new sediments in August 1979 so a continuous year long record was available only from two tanks. Total system apparent production averaged 631 g O_2 per m^2 per year and total system night respiration averaged 462 g O_2 per m^2 per year (Table 4). In contrast to the large variations in production measurements in the field, measurements in the tanks show little variation between tanks. The coefficient of variation for two tanks through the year was 2% for production and 3% for respiration.

Total system metabolism values were not directly comparable to bay values since production includes phytoplankton and wall production, and respiration includes phytoplankton, walls, and benthos. In addition, total system apparent production includes the respiratory drain of the benthos and walls, whereas the bay values include only the plankton. However, correction factors were available for making a more direct comparison between the bay and the microcosms from the eight measurements taken in the microcosms to partition metabolism into various compartments. We have assumed that the metabolism in the water column plus that on the walls of the tanks is equal to that in the water column of the bay under the same surface area i.e. (microcosm phytoplankton plus walls) equals (bay phytoplankton). Microcosm sediment respiration accounted for 35–47% of total system production. If the averaged value of 41% is used and added to total system production, a value of 890 g O_2 per m^2 per year is obtained (Table 4) which compares surprisingly well with bay values, particularly for the West Passage (Table 3). The value of 41% also provides an indication of the fraction of apparent production utilized by the benthos (Table 4). Because the production was so similar in the two systems, this direct measurement of 113 g C per m^2 per year was almost identical to the indirect estimate of carbon available derived from bay survey measurements (Table 3).

Discussion

The bay survey estimations of annual metabolism indicate moderate to high productivity for Narragansett Bay. The highest values occurred in the Providence River with decreasing values down-bay and from the West Passage to the East Passage, in accordance with known nutrient gradients. The widely spaced incubations of this study provided only coarse estimations of metabolism. Large blooms of phytoplankton can appear over a matter of days, particularly in summer, as indicated by the close interval sampling in May (Fig. 2). However, the very large data base has helped to average out large variations, and the results have provided an estimate for annual net production of the bay which seems in line with estimations made for other temperate areas (Table 5).

Our estimates for respiration include the effects of heterotrophic organisms, as the microcosm P/R ratio was based on water column metabolism. Our calculations of the amount of respiration due to zooplankton suggests that this component was a small part of the water column respiration. If we assume that a mixed population of zooplankton consumes 28–56 mg per m^3 of oxygen per night at 20 °C (Vargo 1976) and a water column depth of 5 m, then the oxygen consumption will be 140–280 mg O_2 per m^2

TABLE 5. Annual primary productivity for various areas.

Area	g C/m²/yr	Method	Reference
Georges Bank	400–450	C-14, light gradient incubation	Sherman 1980
St. Margaret's Bay	190 ± 60	C-14, light gradient incubation	Platt 1971
Narragansett Bay	220	Net production based oxygen bottles, *in situ*	Smayda 1973
	308	C-14, light gradient incubation	Furnas et al. 1976
	440	Gross production based on oxygen, light gradient incubation	Vargo 1976, 1979
	99	Simulation model calculation of daytime net production	Kremer and Nixon 1978
	269	Net daytime production based on oxygen bottles, *in situ*	This study
New York Bight			
(25–50 m)	160	Gross productivity calculation based on chlorophyll, light intensity, and extinction coefficient	Ryther and Yentsch 1958
(50–1,000 m)	135		
North Sea	90	C-14, light gradient incubations	Steele 1974

per night. Water column respiration values (annual values divided by 365) varied around the bay between 1.1 to 2.3 g O_2 per m^2 per night and averaged 1.5 g O_2 per m^2 per night (Table 3). Thus on the average, about 14% of the respiration in the water column can be attributed to zooplankton. This estimate of 38 g O_2 per m^2 per yr is on the high side since zooplankton respiration at 20 °C has been compared to mean bay temperature of ~10 °C.

Estimations of the amounts of carbon available for export and to the benthos in the bay and in the microcosms yield values of 110 g C per m^2 per yr and 113 g C per m^2 per yr, respectively. These values can be compared to the measured benthic oxygen uptake for Narragansett Bay (Nixon et al. 1976). A value of 140 g C per m^2 per year was cited based on a respiratory quotient of 1. However, if the conversion factor in Table 1 or a respiratory quotient equivalent to 0.83 is used the value becomes 115 g C per m^2 per year. Considering all the errors inherent in the oxygen measurements, the oxygen to carbon conversion, and the use of the microcosm P/R ratio, such a coincidence is remarkable. We conclude the benthos utilizes almost all of the available carbon.

The agreement between the microcosm and bay values for daytime net production and 24-hour net production suggests that the microcosms have been scaled to the bay remarkably well. Observations in the microcosms also provided useful conversion

TABLE 6. The standing crop of demersal fish compared to the carbon available.

Area	Carbon Available g C/m²/yr	Percent of Annual Net Production	Demersal Fish g C/m²	Percent of Annual Net Production
Narragansett Bay				
(estimate from net production)	110[a]	41[a]	0.3 ± 0.2[c]	0.1[a]
(benthic respiration)	115[b]	43[a]		
MERL Microcosms	113[a]	41[a]	0.4 ± 0.1[d]	0.1[a]

[a] This study.
[b] Nixon, et al. 1976, R.Q. = 0.83.
[c] Oviatt and Nixon 1973.
[d] Oviatt unpublished data from control microcosms, 1979.

factors for daily net production and night respiration which were applied to evaluate bay data (Table 1). It appears that we can learn a great deal about nature by examining the behavior of the microcosms, and by the judicious use of comparisons between them.

The question of demersal fish production derived from the carbon available to the benthos is considered. Some crude estimations have been made by assuming that the dry weight of fish is equivalent to 20% of the wet weight and half of the dry weight is equivalent to carbon (Table 6). The estimation of fish biomass based on survey and tank draindown was in good agreement for the bay and the microcosms. The percent of annual net production, much less than 1%, that this biomass represents was also in good agreement. Even for higher trophic levels, it appears that the microcosms have been scaled well to one natural system. The microcosms may in the future be useful for refining our understanding of how various physical and nutrient regimes result in fish production.

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